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The development of the imbedded antheridium in Dryopteris stipularis (Willd.) Maxon and "Nephrodium molle"*

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(with plates 26–28)

The discovery by Farmer and Digby ('07) of the development of a sporophyte from the essential fusion of two vegetative cells of the gametophyte has aroused a keen interest in the study of apogamy in ferns and other higher plants as well, and has given a somewhat different meaning to the already variously interpreted term, apogamy.

These authors have found that in the prothallia of *Lastrea pseudo-mas*, var. *polydactyla* Dadds, and *Lastrea pseudo-mas*, var. *polydactyla* Wills, developed from normal spores and therefore possessing the gametophytic number of chromosomes, a doubling of the chromosomes was secured in an apogamous embryo by the migration and fusion of vegetative nuclei. The region of migrating nuclei, while not confined to a definite area on a prothallium, was always found to be in the younger portions. The basis of the entire process of the migration and fusion of nuclei was observed to be chemotactic. The elongated migrating nucleus coming in contact with the wall of the receptive cell was seen to slip through an opening, made, probably, by a fermentative action, and fuse with the nucleus of the invaded cell directly or after some time. It is believed by Farmer and Digby that this fusion of the nuclei of adjacent vegetative cells, accompanied by the doubling of the

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* *Nephrodium molle*, according to Christensen (Index Filicum 444. 1905), is a synonym of *Dryopteris parasitica*.

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number of chromosomes, takes the place of the normal sexual fusion of the two gametes.

In addition to the above, the following ferns were studied: *Athyrium Filix-foemina*, vars. *clarissima* Bolton, *clarissima* Jones, and *unco-glomeratum* Stansfield; *Lastrea pseudo-mas*, var. *cristata apospora* Druery; and *Scolopendrium vulgare* var. *crispum Drummondae.* From these five forms, being aposporous, naturally or induced, there resulted prothallia having the double or sporophytic number of chromosomes. Different types of sporophytes were produced from these aposporous prothallia, namely: from the prothallia of *Athyrium Filix-foemina*, var. *clarissima* Bolton, and *Scolopendrium vulgare*, var. *crispum Drummondae*, the embryo arose in each case from an egg-cell, fecundation being unnecessary as the egg-cell already possessed the full complement of chromosomes. While the complete details were not made out for the origin of the embryo produced in *Athyrium Filix-foemina*, var. *unco-glomeratum* Stansfield, the probabilities are that it is like the preceding. The two remaining forms are examples of sporophytic budding. In *Athyrium Filix-foemina*, var. *clarissima* Jones, the sporophyte appears as the direct outgrowth of the apical surface in connection with an endogenous foot. The sporophyte in *Lastrea pseudo-mas*, var. *cristata apospora* Druery, makes its appearance as a small excrescence directly behind the growing point.

Lang ('98) presented a detailed account of the grosser phenomena of apogamous sporophytic outgrowths from prothallia grown from spores. The following fourteen forms are described: *Aspidium aculeatum* Sw., var. *multifidum* Woll., *A. angulare* Willd., var. *foliosum multifidum*, var. *acutifolium multifidum* (no results), *A. frondosum* Lowe; *Athyrium nipponicum* Mett., var. *cristatum*, *A. Filix-foemina* Bernh., var. *percristatum* Cousens, var. *cruciato-cristatum*, var. *coronatum* Lowe; *Nephrodium dilatatum* Desv. var. *cristatum gracile*, *N. Oreopteris*, var. *coronans* Barnes; *Polypodium vulgare* L., var. *grandiceps* Fox; *Scolopendrium vulgare* Sm., var. *ramulosissimum* Woll., var. *marginale.* His results were obtained from experimental cultures of prothallia, watering them only from below and exposing them to bright sunlight, diminishing in this way the frequency of fecundation. The most usual type of sporophytic budding cited in his paper is that of the continuation of the prothallium as a cylindrical process. This process continues as a leaf or bears upon it leaves, roots, and ramenta. Sporophytic growths occur also on prothallia without the intervention of a cylindrical process, or as tracheids in the prothallium or cylindrical process. Sporangia also were observed to occur on the process.

Quite recently a paper has been published by Yamanouchi ('08, III) on apogamy in *Nephrodium*. This details an account of an embryo produced apogamously, with the gametophytic or *x* number of chromosomes. The writer in his previous papers on Sporogenesis and on Spermatogenesis, Oogenesis, and Fertilization in *Nephrodium* showed that under ordinary conditions the life history of this fern was quite orthodox. Under somewhat artificial cultural conditions, *e. g.*, keeping the prothallia rather dry and exposed to bright sunlight, watering only from below, fertilization was prevented. According to Yamanouchi the prothallia grown under such conditions developed slowly with larger cells than those grown under normal conditions. Antheridia were produced in abundance with active sperms, to all appearances capable of fertilizing an egg-cell, and reacting positively to 0.01 per cent. solution of sodium malate (*loc. cit.* 298). The rarely found archegonia were seen to be in a collapsed or poorly developed condition, probably incapable of functioning. The development of the sporophytic outgrowth was observed to be simultaneous with the growth of the archegonial cushion and to originate from a superficial cell in this region, in connection with cells just below it. No migration or fusion of nuclei was observed. The cells that comprise the apogamous embryo are distinguished from the cells of the prothallium by their smaller size, their relatively larger nuclei and denser cytoplasm. There is described here an embryo with the gametophytic number of chromosomes, arising from a single superficial cell and the vegetative cells beneath it, differing only in appearance from a normal embryo by the absence of the foot. This is the first case recorded of an apogamous embryo with the alleged gametophytic number of chromosomes.

During the autumn of 1908 several fine specimens of a southern fern,* *Dryopteris stipularis* (Willd.) Maxon, which were being grown in the greenhouse of the botanical laboratory of Indiana University, were placed at my disposal, with the suggestion that a study of the embryology be made with the view of ascertaining whether apogamy existed or could be induced in this species. Through the kindness of Mr. Alois Frey, a number of fruiting fronds of "*Nephrodium molle*" were obtained from the Lincoln Park Gardens, Chicago, from which cultures were also made and the prothallia studied in regard to the same problem.

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* The original specimen was brought from Cuba by Prof. C. H. Eigenmann.

METHOD OF CULTURE

Spores were sown upon sterilized soil in shallow earthen saucers. These were then placed in larger saucers of about the same depth. The cultures were watered with just enough distilled water after the spores had germinated to allow the prothallia to grow slowly. Water poured into the outer dish soaked up very slowly through the inner dish into the soil. This regulated the rapidity in the absorption of water by the soil and prevented the cultures from being alternately dry and moist. Evenness of moisture in the soil was further effected by placing a bell jar upon small blocks of wood, about one inch and a half high, above each culture. This allowed free circulation of air around the culture. This method prevented the collecting of moisture upon the dome of the bell jar and falling upon the culture, thereby making fertilization possible. The bell jars further protected the cultures from spores of fungi, etc. The prothallia grown under such conditions grew slowly but thrivingly. A glance at a culture presented the picture of a deep green carpet; closer inspection revealed the prothallia to be large, much larger than those, on which, under normal culture, embryos appear. No sporophytes occurred on the prothallia grown under these conditions. Material was fixed from time to time in chrom-osmic acetic and chrom-acetic acids. Prothallia were washed, dehydrated, and imbedded in paraffin. Sections were cut 5 and 6 microns in thickness and stained in safranin, Bismarck brown, and gentian violet. A detailed account of observations on each fern will now be given.

I. DRYOPTERIS STIPULARIS (Willd.) Maxon

Upon examining the sections, the prothallia were found to be unusually large. The archegonial cushion presented, in most cases, a thickness twice as great as that of the normally grown prothallium; the apical sinus consisted of a large number of apical cells as seen in the consecutive sections of a prothallium. The wings were correspondingly large and somewhat wavy-margined. The entire prothallium, not having its period of functioning and usefulness ended by the production of a sporophyte, appeared overgrown in all directions. Archegonia and antheridia were produced on the upper as well as the lower surface. It is in the actively growing portion of the prothallium, *i. e.*, the vicinity of the apical sinus that one would look for some manifestation of apogamy. Well up in this region of the prothallium a structure was seen in a position to suggest an apogamous embryo, but this proved to be an imbedded antheridium (*figure 7*). Normal, as well as one or more imbedded, antheridia were found on the same prothallium. The initial cell of an imbedded antheridium is not distinguished in any way from the initial cell of an archegonium. The first wall laid down in the development of an archegonium is a periclinal one cutting off the initial cell of the neck. In a deep-seated antheridium the first division is likewise periclinal. The outer or superficial cell forms the cover, while the inner cell gives rise to the spermatogenous tissue. In all cases thus far observed, the second division of the inner cell of such an antheridium is an oblique one (*figure 1*). The resulting cells in this instance were unequal. In other cases, the division, also oblique, resulted in more nearly equal cells, as in *figure 2*. The nuclei in these cells were large, the cytoplasm dense and granular, and in staining characteristics typical of cells in young archegonia or antheridia. Three almost equal cells are seen in a developing antheridium in *figure 3*. Further divisions now take place in three planes until the structure becomes quite massive (*figures 4–7*). In *figures 5* and *6*, the identity of the structure is shown in its shrinking away from the surrounding cells. The proximity of these developing imbedded antheridia to the apical region is seen in *figures 1, 2, 4, 5*, and *6*. In *figure 7* is pictured the most typical form of a deep-seated antheridium. This is globular, projecting slightly above the surface of the prothallium. As the antheridium nears maturity the tendency to bulge outward is more pronounced. In the earliest stages the antheridium is usually even with the surface of the prothallium, and it may remain so when mature (*figure 9*). *Figure 8* shows a form of antheridium occasionally met with. There is here a slight projection above the surface of the prothallium. This antheridium is peculiar in that it extends so deeply into the prothallium.

There seems to be no definite method for the further divisions of the outer cell. In sections, two or more cells are seen in the cover, irregular in size and depth. From this it will be seen that there is no definite arrangement or number in the cells comprising the cover. In most cases the antheridium was situated under one layer of cells, occasionally under two layers (*figure 10*). There was a marked variety in the size of imbedded antheridia. All degrees of size and shape were found from those about as large as the superficial type and rather globular to those more than twice as large and very irregular in shape (*figures 7–9*). The finding of imbedded antheridia upon these prothallia was not an occasional thing but a common occurrence, the majority of the prothallia grown under the above-detailed conditions bearing one or more imbedded antheridia. As a rule these were found upon the largest prothallia, although occasionally one was seen on a smaller prothallium. These deep-seated structures were always found to be in the apical region or within a few cells of it.

Typical of cell divisions in normal antheridia, the cells in the imbedded type divide simultaneously. The development of the sperms in the imbedded antheridium was followed closely and was found to differ in no way from that of the sperms in normal antheridia, a sperm from an imbedded organ appearing exactly like a sperm from a superficial one. Owing to the occurrence of both normal and imbedded antheridia on the same prothallium and the similarity between the sperms, sperms from a deep-seated antheridium could not be isolated.

In *figure 11* is seen a section of a prothallium immediately back of the apical region, in which are two imbedded antheridia and a normal archegonium. More than one half of the antheridium, the lower one in the figure, consists of sperm mother-cells, the rest of the antheridium being made up of four large cells. These cells have the granular cytoplasm characteristic of developing sex-cells. Another case similar to the foregoing was observed (*figure 10*), in which instance the antheridium, also in the apical region, was imbedded under two layers of cells. Approximately half of this antheridium consisted of mature sperms, the other half, that nearer the surface, was composed of three cells, two smaller and one very large with a corresponding large nucleus. This last cell bore a striking resemblance to an egg-cell.

The development of the imbedded antheridium is very similar to that of the antheridium in a lower order of ferns as described by Campbell ('07) in the Ophioglossaceae, with the exception of the first divisions and the development of the cover-cell. An approach to the imbedded antheridium of *Dryopteris stipularis* and "*Nephrodium molle*" is found in the antheridium of *Ceratopteris* (Engler & Prantl, Nat. Pflanzenfam. '02). This antheridium projects but slightly above the surface of the prothallium, although it has the customary lid- and ring-cells. The basal cell, assuming a more irregular shape, is designated as the pedicel-cell.

II. "NEPHRODIUM MOLLE"

The origin of the imbedded antheridium in "*Nephrodium molle*" is similar to that of an archegonium and not unlike that described for *Dryopteris stipularis*. After the first division of the initial cell into the outer and inner cells, the inner cell divides periclinally into two unequal cells (*figure 12*), recalling the development of an archegonium. If a division of the larger cell should take place obliquely, a condition would be found as shown in *figure 13*. Further divisions of the two inner cells give rise to the condition seen in *figure 14*. That such structures would develop into imbedded antheridia seems positive. The structure shown in *figure 24*, for example, may have originated in a manner similar to that of an imbedded antheridium, but it is certain that none of these structures would become sporophytes.

These developing structures found in the apical portion of the prothallia will be seen to be similar to the early stages in the development of the imbedded antheridium of *Dryopteris stipularis*. *Figure 14* in "*Nephrodium molle*" could represent an early stage in the development of *figure 8* in *Dryopteris stipularis*. The cells in these structures differ markedly from the surrounding cells in their granular cytoplasm and large nuclei. In *figures 12–14*, the nuclei of the cover-cells have recently divided, whereas the nuclei of the inner cells are in a resting stage. A typical imbedded antheridium similar to those found in *Dryopteris stipularis* is seen in *figure 15*. It projects slightly above the surface now but probably did not in its earlier stages. Three cells of the cover are shown in the section. The developing sperms are quite normal, the cells having rounded up, with the blepharoplast showing plainly in some of them. As was the case in *Dryopteris stipularis*, both kinds of antheridia appear on the same prothallium. In some cases an imbedded antheridium will be seen very near a superficial one. In *figure 16*, a small imbedded antheridium is seen adjoining one of the superficial type. There is a slight variation in the basal cell of this last antheridium, inasmuch as it has redivided until it consists of at least three cells. In the imbedded antheridium are a few almost mature sperms, lying loosely in the antheridial cavity. Two very narrow cells are at the base of this antheridium. It is very often the case that some of the cells immediately surrounding the antheridium are narrow. An antheridium, which had a deep-seated origin but in its development projected considerably above the surface of the prothallium, is pictured in *figure 17*.

Figures 18 to *24* comprise a series of drawings from consecutive sections of one prothallium. There are three structures here whose origin is similar to three adjacent archegonia. In *figure 18* two cells with the superficial or cover-cell are seen. The wall separating these two cells is diagonal, recalling a similar condition in *Dryopteris stipularis* (*figure 2*). This in itself is an irregularity for the normal division of an archegonium initial. The next section (*figure 19, a*) shows the same two cells; the innermost cell is a little the larger as is seen in the successive sections. This first structure contains, in all, four cells (*figures 21–23*). The other two cells are also divided by a diagonal wall, the position of this wall being at right angles to the wall separating the first two cells. The wall dividing the two pairs of cells is in the plane of the page. The beginning of the second structure is seen in *figure 19, b*. It appears here as a little hump of three cells, part of the cover. The next section (*figure 20, b*) shows that beneath this cover are two cells, one projecting up into the little hump. In *figure 21, b*, these cells are seen plainly with their large nuclei. The similarity between this and the two-celled stage of an archegonium is striking. Below these two cells in the second structure (*b*) are three more cells (*figures 21–23*, *b*). In these three cells, of which all three nuclei are seen, one cell is superimposed on the one below, the two nuclei appearing one above the other. The wall of the third cell is indicated by the dotted lines. The second structure (*b*) consists therefore of five cells, lying beneath a cover which arches slightly upward.

The third structure (*c*) is first seen in *figure 21*, *c*. Three small cells here project slightly at the left of the second structure (*b*). The next section (*figure 22*, *c*) shows this projection, corresponding to the neck of an archegonium, to be much larger. In this figure are seen three cells belonging to the third structure. The cells of the three formations are seen here (*figure 22*) to lie together as one mass of actively growing cells. From their position in the apical region of the prothallium and from their dissimilarity to the surrounding cells, *i. e.*, their granular, densely staining cytoplasm, large nuclei and absence of chloroplasts, these structures undoubtedly came from potential sex-cells. *Figure 23*, *c*, shows a section cut through the so-called neck of the third structure. Two small cells are seen in the neck-like projection, beneath which are three cells (*figures 23*, *24*, *c*). Below these three cells are two more, making a total of nine in this structure (*figure 24*, *c*). The character of these last two cells justifies the opinion that this structure is of archegonial origin. The two cells mentioned seem to correspond to an egg- and ventral canal-cell of an archegonium.

The cultures of "*Nephrodium molle*" presented the same general characteristics as those of *Dryopteris stipularis* grown under these conditions, differing only in the rapidity of growth, these prothallia not growing quite so slowly as those of *Dryopteris stipularis*. No apogamous sporophytes were found on these prothallia.

GENERAL CONSIDERATIONS

From the foregoing description of the structures obtained through varying the normal cultural conditions, it will be seen that the prothallia of *Dryopteris stipularis* and "*Nephrodium molle*" present a remarkable mobility. As dryness and the exposure to direct sunlight were the only cultural changes from the normal state, the results obtained may be attributed to those causes, none of these structures being found in the normal control cultures. The fact that one form of the expression of the potentialities of these prothallia is that of a deep-seated antheridium is of interest from a number of standpoints. Morphologically the imbedded antheridium is interesting, in that its origin and development is very similar to the origin and development of the normal antheridium of a much lower order of ferns. The detailed development of the antheridium in the Ophioglossaceae (Campbell '07) is essentially similar to the development of the imbedded antheridium as found in *Dryopteris stipularis*. The position of these antheridia in the actively growing part of the prothallium is evidence of the manifestation of an active response to a forced environment and not a condition due to degeneracy or a reversion to more primitive characters. The presence of normal antheridia on the same prothallium bearing the imbedded kind shows that, while the conditions are equal for producing either, the condition of dryness is essential for the formation of the deep-seated antheridium. The imbedded antheridium in the dry cultures was not an occasional occurrence, as one and frequently two or three were found on the majority of the prothallia.

That the response to this dry condition was the production of imbedded antheridia, shows the far-reaching effect of such an environment, as well as the success of the prothallia in combating it. A superficial organ on a prothallium grown in dryness is more in danger from drought than one deeper in the prothallial tissue. To protect the antheridia from the disasters of drying out and thus becoming incapable of functioning, an antheridium has been developed, completely imbedded in the prothallium. Deep seated in its origin and development, such an antheridium is protected from the effects of drought, obtaining from the surrounding prothallial cells the maximum amount of moisture supplied the plants. The improbability of a sperm from a superficial antheridium reaching an egg is apparent in these prothallia due to the lack of the necessary medium, *i. e.*, water. If there could be an internal way for the sperm to reach an egg, another suggestion of the meaning of the imbedded antheridium would be evident. If the migrating and fusing nuclei, producing the apogamous embryo as described by Farmer and Digby, could be traced to such sexual elements as might mature into a deep-seated antheridium or an archegonium, the adaptation there would be more complete. The morphological position of an imbedded antheridium, then, can be regarded as only the expression of the potentialities of the plant, one evidence of the response to environmental conditions.

The sperms from either antheridium apparently differ in no particular. There was a greater variation in the number of sperms in the imbedded antheridia than in those of the normal type, the imbedded antheridia being larger on the whole than the superficial ones. The individuality of the deep-seated antheridium is shown in its slight shrinkage from the surrounding cells.

The case of the imbedded antheridium in which half consists of mature sperms and the other half of three large cells, one resembling very much an egg-cell (*figure 10*), presents another standpoint from which these structures may be considered. This is the subject as to the determination of sex. The question arises, has any cell of a prothallium destined to be a sex-cell the potentialities of either sex? When we remember that these are monoecious prothallia, that each cell came from a spore and that all spores are alike, it would seem as if there were some basis for such a supposition. If we accept this supposition as true, the earliest stages of the imbedded antheridium may be interpreted as the earliest stages of an archegonium. After the first division of a superficial cell into an inner and an outer cell, the inner cell instead of developing into an archegonium becomes the initial of a deep-seated antheridium. The origin of the case above cited may then be explained as a sex-cell, the potentialities of either sex being almost equal, so that half of the structure consists of sperms or the male element, and the other half, composed of three cells, one especially resembling an egg-cell, represents the female element.

Another case, the lower antheridium in *figure 11*, is shown where more than one half of the structure consists of sperm mother-cells, the rest of the antheridium being taken up by a number of large cells, which may represent the female element of the original cell. The fact that maleness dominates in these structures and that imbedded antheridia are the result of dryness and not abortive archegonia, may be due to the amount of moisture supplied. In dioecious ferns the archegonia are found on the larger prothallia, the antheridia on the smaller. Good cultural conditions may favor the probability of a destined sex organ, female; poor cultural conditions, male, although experimental evidence is conflicting on this point.

While the data are not so complete for "*Nephrodium molle*" as for *Dryopteris stipularis*, less material of the former having been prepared and studied, the origin of the imbedded antheridium found in this fern is undoubtedly similar to that of *Dryopteris stipularis*. That the structures seen in *figures 12–14* would develop into imbedded antheridia can not be definitely stated, but that deep-seated antheridia could originate in this manner is certain. A more exhaustive study of both ferns may bring out more facts. Normal antheridia, imbedded antheridia, and a transitional stage (*figure 11*) where an antheridium had a deep-seated origin but in its development projected beyond the surface of the prothallium, were all found in "*Nephrodium molle.*"

The condition represented in *figures 18–24* is a different expression of "*Nephrodium molle*" under a dry state. The origin of the structure (*c*) in *figures 22–24*, at the base of which are the apparent egg- and ventral canal-cell, is without question a cell which under normal conditions would have given rise to a normal archegonium. The impossibility of this egg being fertilized, due to its position and the improbability of a sperm being attracted to it, is obvious. What the other two structures would give rise to is unknown. That they might produce egg-cells is a possibility, or that they might become imbedded antheridia is also to be considered.

It is impossible to draw any parallel between the imbedded antheridium of these ferns and the antheridium of *Ceratopteris*, the latter being borne on an aquatic fern, and structurally similar to the ordinary antheridium.

No apogamous sporophytes were found in the cultures of either fern. In anticipating the production of apogamy in these ferns, a type of sporophyte was expected similar to that described by Lang, *i. e.*, sporophytic budding from the prothallium or upon a process from the prothallium. If the sporophytes produced from the spore-grown prothallia of Lang do not originate from vegetative fusion of nuclei, their life history, as far as the number of chromosomes is concerned, is similar to the life history of the apogamous "*Nephrodium molle*" described by Yamanouchi. The figures of Yamanouchi, illustrating the development of this apogamous embryo, are not convincing. There is no evidence that the shaded cells in his figure 1 (*loc. cit.* 299) develop into the embryo shown in figure 29 (*pl. 10*). If apogamy is present in "*Nephrodium molle*," this plant shows greater potentialities than *Dryopteris stipularis* at the present time. A study of just how much dryness will cause the development of imbedded antheridia and how much will bring forth apogamy seems desirable.

While the main object in carrying on this investigation, namely, to obtain apogamy, has not been accomplished, an antheridium has been found that, so far as the writer knows, has not been obtained before. Acknowledgment is due here to the courtesy of Professor D. H. Campbell, who confirmed the above opinion as to the newness of such an imbedded antheridium in the higher ferns.

I wish to express my deep gratitude to Dr. David M. Mottier for his constant advice and encouragement throughout this study.

CONCLUSION

At the present time I have found no apogamy in either *Dryopteris stipularis* or "*Nephrodium molle*," although, as far as I was able to determine, the cultural conditions described by Yamanouchi were repeated. An imbedded antheridium similar to the antheridia of lower ferns was found on the majority of the prothallia of *Dryopteris stipularis* and on a number of the prothallia of "*Nephrodium molle*." In *Dryopteris stipularis*, in addition to imbedded antheridia, deep-seated structures were found, half of which consisted of sperms and the remainder of large cells. In "*Nephrodium molle*" a deep-seated egg- and ventral canal-cell were found.

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Explanation of figures in plates 26–28

All figures were drawn with the aid of a camera lucida, using homogeneous oil-immersion objective 2 mm. combined with ocular 4.

1–11. *Dryopteris stipularis*

1. Two-celled stage of an imbedded antheridium in the apical sinus.

2. Similar stage as above, the antheridium projecting slightly above the surface of the prothallium. The two cells are more equal in size.

3. Three-celled stage of an imbedded antheridium.

4. Young stage in the development of an imbedded antheridium. Apical cell not shown.

5. Stage similar to that in fig. 4. Antheridium shows no projection from the prothallium.

6. Antheridium in the apical portion, showing slight shrinkage from the surrounding cells. Relative density of cells in antheridium and in the prothallium is seen. Figs. 1, 4, and 6 indicate the width of the cushion.

7. Globular imbedded antheridium, causing a slight mound on the surface of the prothallium.

8. Wedge-shaped antheridium projecting deeply into the prothallium. Cytoplasmic contents of cells beginning to round up.

9. Large mature antheridium, not projecting from the prothallium at all. Irregular outline of antheridium is seen.

10. Deep-seated antheridium in which only half has developed into sperms. The other half consists of three large cells, one, that nearer the surface, resembling an egg-cell. This antheridium is situated under two layers of cells. The cover of those pictured in figs. 1–9 consists of but one layer of cells.

11. Section showing two imbedded antheridia and a normal archegonium in the apical region. The lower antheridium in the figure consists partly of sperm mother-cells. The remainder is made up of four large cells.

12–24. *Nephrodium molle.*

12. A structure, similar to a young archegonium, which may be the beginning of an imbedded antheridium.

13. An older stage. This could represent a stage in the formation of an imbedded antheridium.

14. A five-celled, deep-seated structure similar to a step in the development of imbedded antheridia. The densely granular cytoplasm and large resting nuclei are indicated.

15. Imbedded antheridium, projecting slightly. Cells beginning to round up.

16. Small imbedded antheridium, with almost mature sperms, adjacent to a superficial one.

17. An antheridium of deep-seated origin, projecting half way above the surface of the prothallium.

18. Two cells under a cover-cell *a* of a deep-seated four-celled structure. This and the following figures are from consecutive sections of a prothallium.

19. The same two cells of structure *a* are seen. Three cells in the cover of structure *b* project slightly from the surface.

20. More cells of the cover of structure *a* are seen. The lower cell of the first pair is below this cover. In structure *b* there are two cells, one projecting up into the cover.

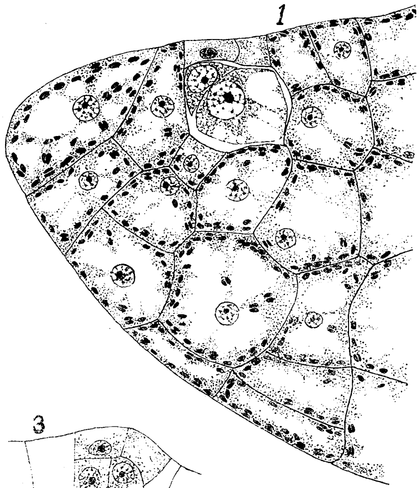
21. The beginning of the third structure *c* is indicated here by three small cells, part of the cover. Two cells of structure *b* show. In structure *a* the second pair of cells, with the wall dividing them at right angles to the wall dividing the first pair fig. 19, *a*, is seen.

22. The cells of three structures appear as one contiguous mass of actively growing cells. Both nuclei of the second pair of cells of structure *a* are present. In structure *b* three cells in addition to those already described are seen beneath them. The cover of structure *c* projects considerably above the surface. Only three cells of this last structure show.

23. Structure *a* presents about the same appearance as in the preceding figures. Two cells of structure *b* are visible. This section passing through the neck-like projection of structure *c* discloses two small cells in it. Beneath this are four cells.

24. The two lowest cells of structure *c* are seen to resemble strikingly an egg- and ventral canal-cell. Above this so-called ventral canal-cell, three cells appear, two of which were present in fig. 23, *c*. Structure *c* consists, then, of nine cells, running through figs. 21–24. The cells in these three structures differ from the surrounding cells in their granular contents and large nuclei.

1



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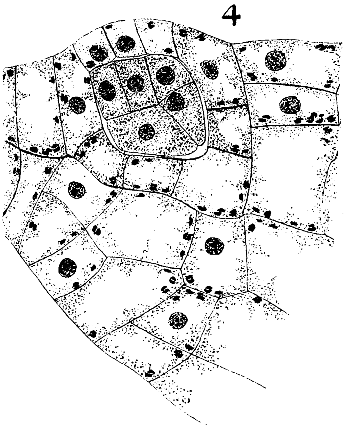

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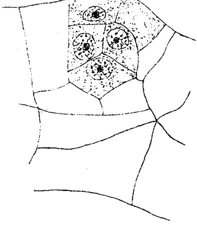

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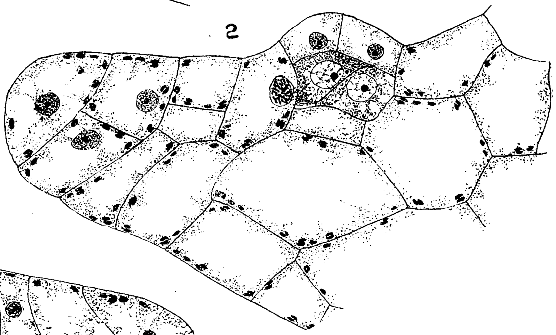

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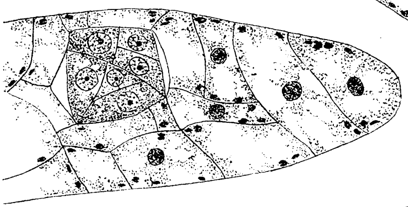

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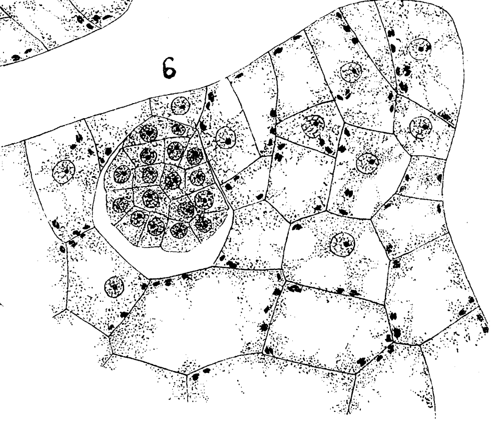

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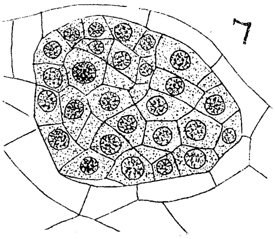

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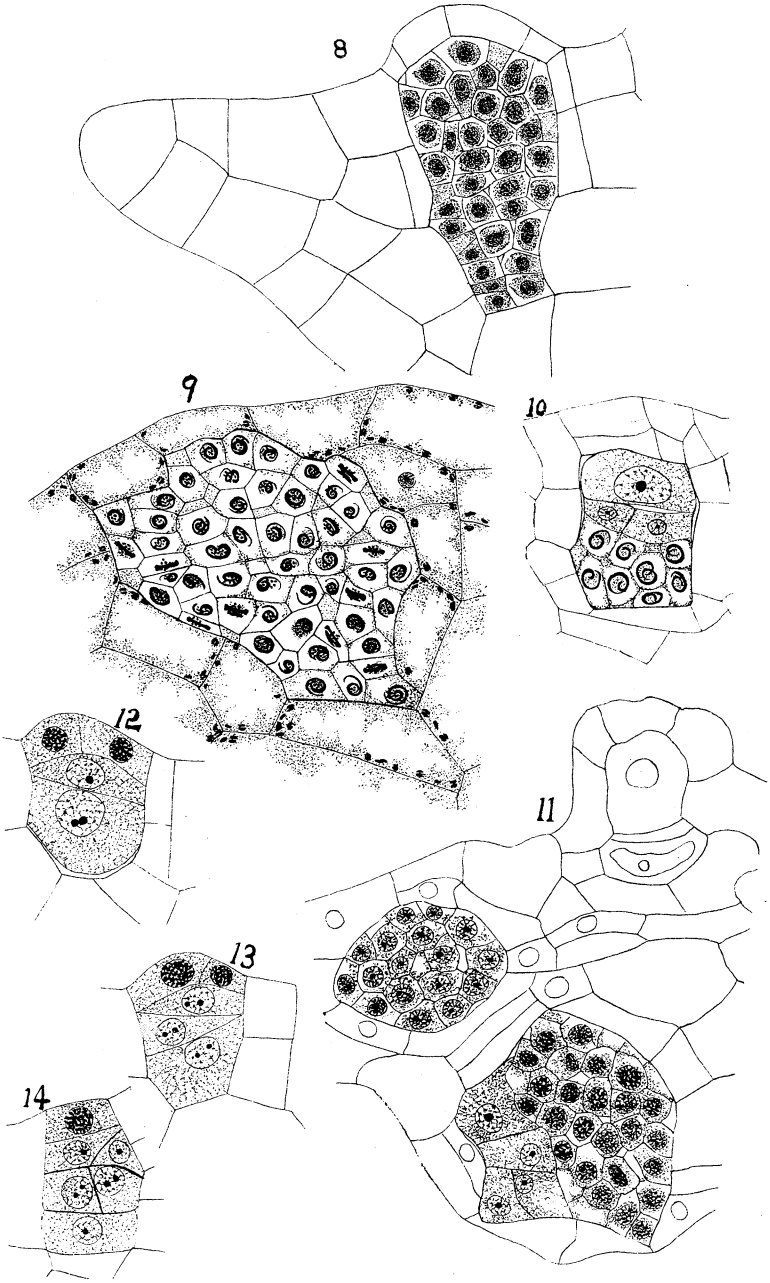
BLACK, THE IMBEDDED ANTHERIDIUM IN DRYOPTERIS STIPULARIS, ETC.

COCKAYNE, BOSTON



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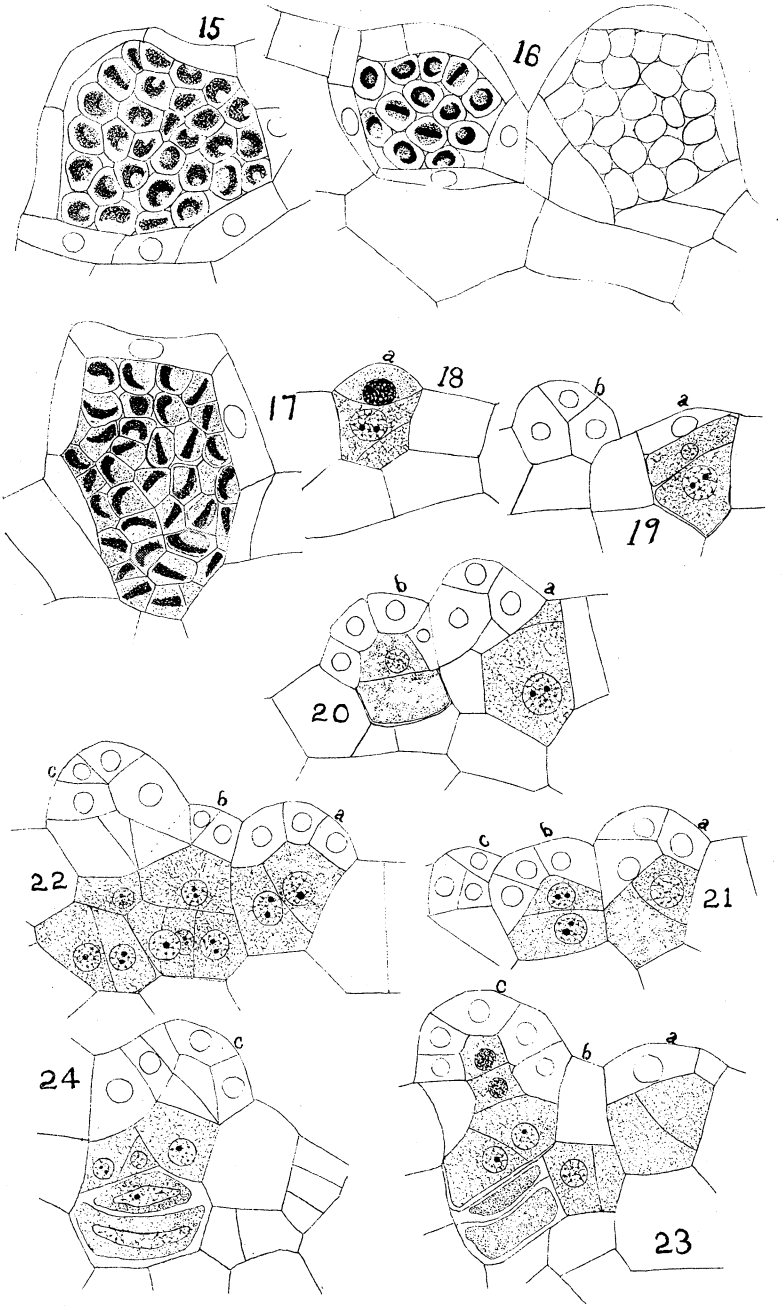
COCKAYNE, BOSTON



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